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S.P.R.I. fr Brian Roberts

RESULTS OF THE NORWEGIAN SCIENTIFIC EXPEDITION
TO TRISTAN DA CUNHA 1937—1938. No. 22

A POLLEN-ANALYTIC INVESTIGATION OF TWO PEAT DEPOSITS FROM TRISTAN DA CUNHA

BY
ULF HAFSTEN

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BY

ULF HAFSTEN

WITH 5 FIGURES IN THE TEXT AND 2 PLATES

PREFACE.

Being aware of the extremely interesting problems concerning the vegetation of the subantarctic islands and its history I wish to thank Dr. ERLING CHRISTOPHERSEN who placed this valuable peat and plant material at my disposal for investigation.

Likewise, I owe a deep debt of gratitude to Professor K. FÆGRI who was willing to teach me the methods of pollen analysis and who has always gladly and freely given his help and advice at all stages of the work.

I also wish to thank Mr. LARS HAALAND for reading and correcting the manuscript from a meteorologist's standpoint and Mr. PHILIP TALLANTIRE who has translated the Norwegian text.

It is most unfortunate that these valuable peat samples from Tristan da Cunha have remained uninvestigated for over ten years. This has led to a substantial reduction in their scientific value so that only two out of the six bog profiles were found to be fit for pollen analytical investigation.

Botanisk museum, Bergen, in November 1949.

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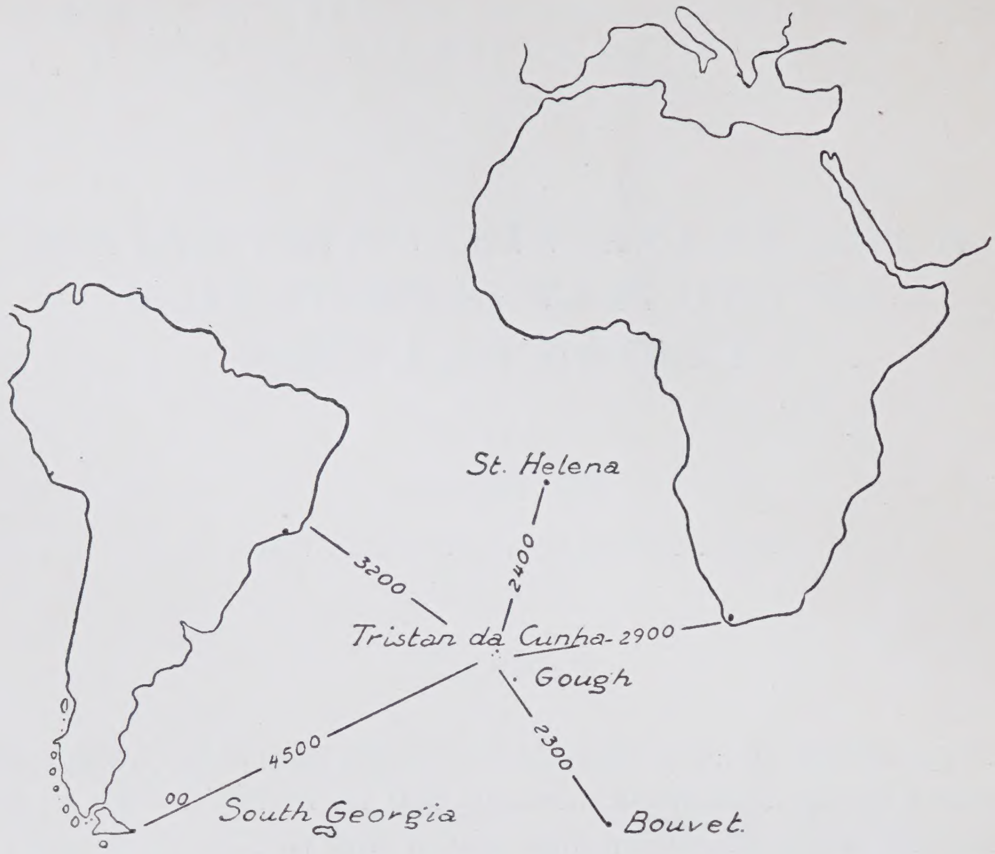

Fig. 1. Sketch map showing position of the Tristan da Cunha group. Distances in kilometres (After Dunne 1941).

A. GEOGRAPHY OF THE AREA

1. POSITION AND TOPOGRAPHY.

A detailed geographical description of the Tristan da Cunha group of islands is given in the "Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937—38 vols. I, II" (Christophersen 1946). For the present work the isolated position of the island group on the "Atlantic Ridge" at latitude c. 37° S and longitude 12° W is of particular interest. Fig. 1 shows the distance, in kilometres, of Tristan da Cunha from the nearest islands and continents. Fig. 2 shows the relative position of the individual islands within the Tristan group.

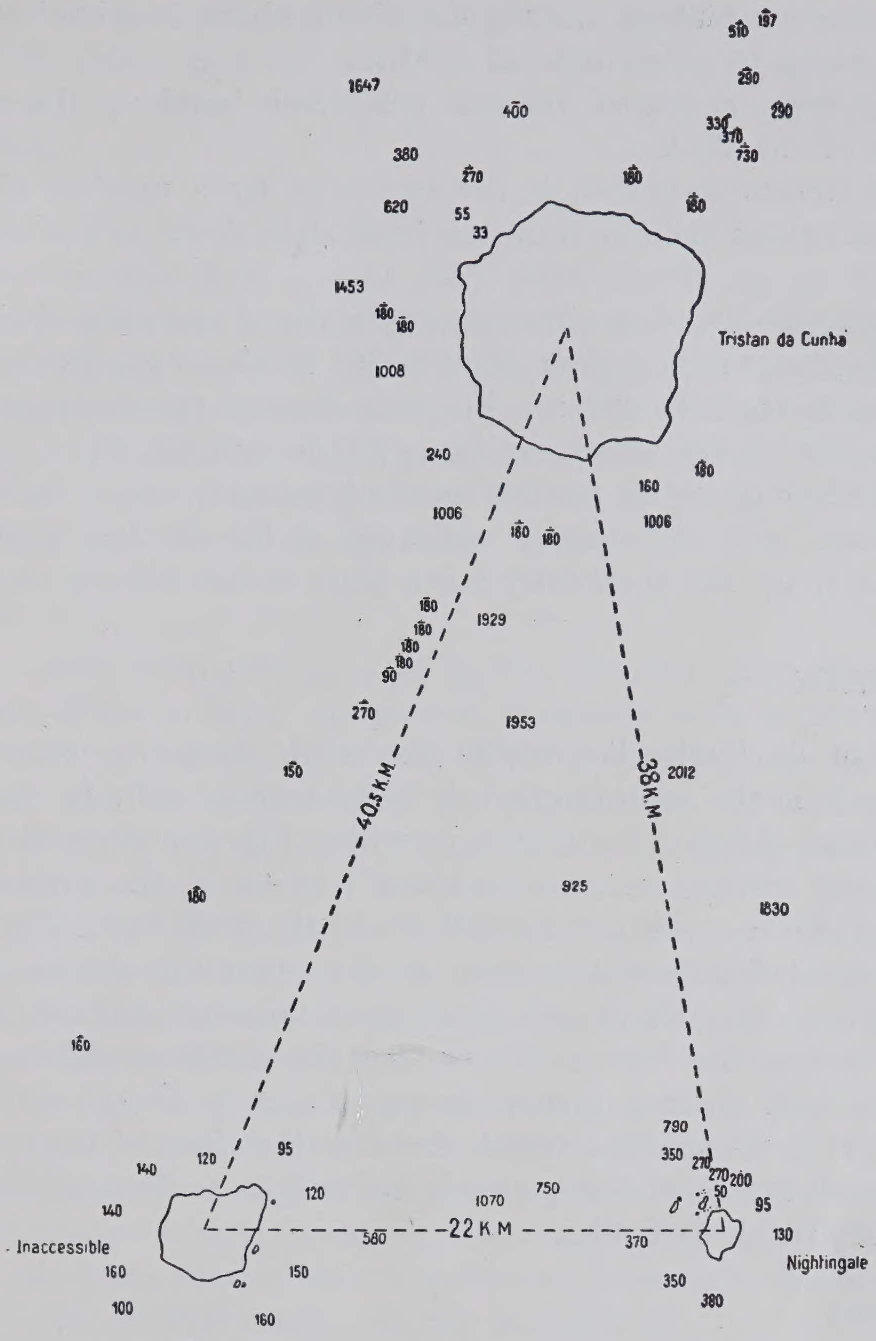

Fig. 2. Tristan da Cunha group of islands (After Dunne 1941).

The topographic features of Main Island can be summarised as follows (cp. fig. 3):

1. A narrow coastal plain, unbroken by bays or other inlets.
2. Precipitous slopes rising from this narrow plain to 500 metres above sea level.

3. The Base, a plateau girdling the island, about 2—3 km in breadth and rising to an altitude of 1000 m.
4. Steep scree slopes of volcanic ash which build up the volcanic cone of the Peak.
5. This structural system is deeply scored by a number of gullies which extend radially from the Peak right down to sea level.

Nightingale Island consists topographically of two areas of highland, one in the east whose highest point is 365 m above sea level and one in the south reaching 290 m. The area around the Swampy Lakes, where profile 15 was taken, lies at c. 200 m (cp. fig. 4).

The island group is further more of volcanic origin, believed to be associated with the orogenic upheavals in the Tertiary period. No volcanic activity has apparently taken place within historic time.

2. CLIMATE.

Tristan da Cunha lies within the south temperate zone at the transition from the subantarctic belt to the tropical belt. In the winter period (June—August) the islands lie within the westerly cyclone belt, the "roaring forties" or "the variables", whilst in the summer (December—February) this cyclone belt lies to the southward. The scanty meteorological data available seem to show that the climate has the character to be expected of such an inter-zonal position, and can probably be explained on the basis of the existing circulation conditions around the strong high pressure system at approximately Tristan da Cunha's position. It is reasonable to think that also the effect of the cold Cape Horn-current must be of importance towards an understanding of the climate of Tristan da Cunha.

Temperature.

Carmichael as early as 1818, mentions Tristan da Cunha's mild climate, where a seldom and transient ground frost, insufficient to seriously set-back the vegetation, is the only witness of winter. Having an annual mean temperature of + 14.5° C — average summer temperature + 18° C with a maximum temperature of + 24.8° C and an average winter temperature of + 12° C with a minimum temperature of + 4.5° C, all measured in 1938 — the climate can be described as warm temperate oceanic with relatively little temperature variation between summer and winter. The temperature naturally decreases with altitude and the Peak is usually snow-covered during the winter. All the available observations show that practically speaking the temperature never falls below freezing point in the lowlands, though hailstorms can occur in winter and spring and do damage to both dwellings and crops.

Wind.

The available data suggest that wind conditions on Tristan da Cunha are somewhat variable but that the prevailing windquarter is westerly, varying from NW to SW. The islands must be characterised as stormswept and especially in the winter months are often exposed to sudden and violent storms. The summer period is usually less windy. Wind is certainly a limiting factor for vegetation, in particular for forest, on Tristan da Cunha (cp. GOOD 1947 p. 284).

Rainfall.

It is difficult to give accurate figures, however, since there are so few observations to hand. At present it appears to be a frontal effect, at the boundary between the great westerly wind currents at c. 40°—50° S lat. and the northwesterly air current from the region of high pressure at about the same latitude as Tristan da Cunha, that produces the cyclonic precipitation over the islands. Because of the mountainous nature of Tristan da Cunha the rainfall is further increased as the air masses are forced upward over the mountains. According to meteorological calculations the air masses, under conditions of 80 % relative humidity and a monthly mean temperature of 11° C to 19° C, need rise no more than 450 m at maximum before condensation takes place. Thus a heavy rainfall results at least on the windward side of the mountains, and mist banks form higher up, certainly the Peak veiled in a thick encircling blanket of mist (cloud-cap) is a characteristic sight. Nightingale, which is much less mountainous than Tristan, presumably has a markedly lower rainfall, probably only cyclonic precipitation.

A few rainfall figures from the settlement 1938 (CHRISTOPHERSEN 1946 No. 10) will give some idea of the conditions:

Total rainfall	1751,0 mm	
Highest monthly total	339,5 mm	(May)
Lowest monthly total	26,3 mm	(January).

The figures increase with altitude, such that the Base has 1½ times and the Peak 3½ times so much rainfall as the lowland. The summer is plainly drier than the winter, the autumn and winter rainfall being more than twice as much as the spring and summer rainfall.

The distribution of rainfall is of prime importance for the development of the vegetation and bogs and observations from 1907—9, 1923—4 and 1938 show firstly that the rainfall appears to be evenly distributed within the different seasons, secondly that it falls mainly in more or less heavy downpours and that steady drizzly rain is seldom. The tables show for example astonishingly few wholly sunless days with continuous rain. CARMICHAEL (1818 p. 492) has already drawn attention to this fact.

The average value for cloudcover (cloudiness) in January and February 1938 was 7.2 for both months.

3. VEGETATION.

Those botanists who have visited Tristan da Cunha up to the present day have been more interested in the special phytogeographical (chorological) problems it presents than in ecological studies. This constitutes a decided handicap owing to the difficulty inherent in constructing, let alone interpreting the pollen diagrams without a certain knowledge of the various plant communities and their ecology to act as a guide. To try and compensate for this want I have attempted provisionally to construct a broad picture of the most important plant communities found on the islands. This is based on 1. personal information from Dr. CHRISTOPHERSEN, 2. study of herbarium material from Tristan da Cunha, and 3. the literature about this group of islands and other islands in the subantarctic ocean. In the course of my work I have encountered many interesting phytogeographical problems connected with those genera with which I dealt. In passing it may be mentioned that the literature concerning the distribution of these genera has given me much useful information about their ecology. A striking example is the marked similarity in the vegetation and its development on Tristan da Cunha and Masafuera in the Juan Fernandez island group in the same latitude (SKOTTSBERG 1945 p. 152).

Main Island.

The vegetation appears to be divisible into 6 zones:

I. Strand vegetation.
2. *Phylica-* forest (Forest zone).
3. *Blechnum palmiforme* scrub (Tree-fern zone).
4. *Rumex-Holcus* grassland (Subalpine zone).
5. *Empetrum rubrum-Rhacomitrium* heath (Alpine zone).
6. Sparse *moss-lichen* cover (Alpine zone).

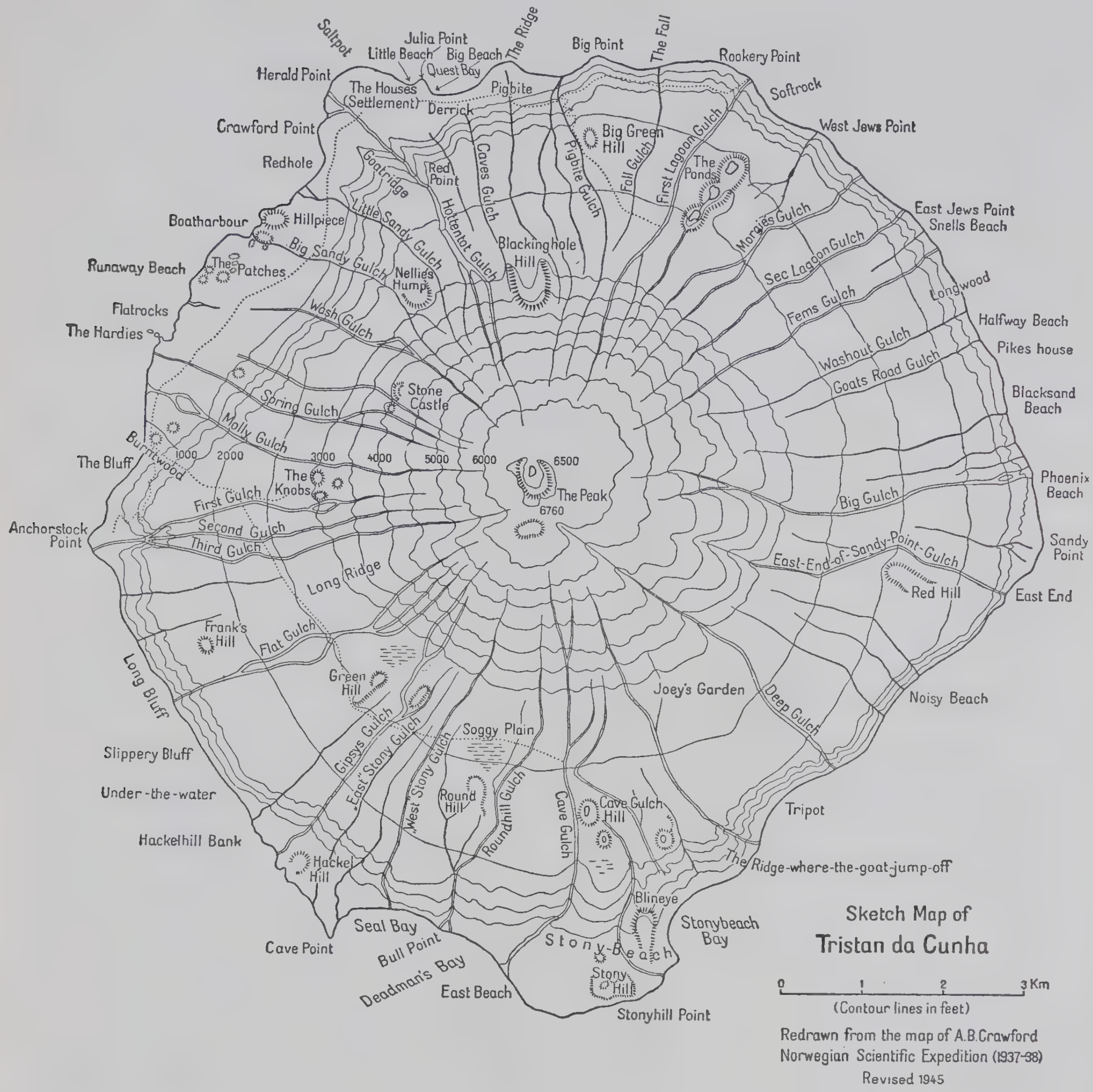

Fig. 3. Sketch map of the Main Island. Contour lines in feet (After Dunne 1941).

1. *Strand vegetation.*

The facts are regretably few but they suggest that the vegetation can be composed of many of those species which grow at the lower and moderate altitudes (cf. Masafuera): *Apium australe, Chenopodium tomentosum, Chevreulia sarmentosa, Convolvulus Soldanella, Gramineae, Rumex frutescens, Scirpus-* spp., *Spartina arundinacea* (which is found in dense stands from the upper strand-zone up to an altitude of 6—700 m), *Adiantum, Asplenium,* etc.

2. *The Forest zone,* up to c. 750 m level.

Phylica arborea, a deciduous tree of the family *Rhamnaceae,* is the only tree growing wild on the islands; it forms a continuous belt of forest around the whole island except in the vicinity of the settlement where the forest has been cut for fuel and cleared for grazing.

The upper tree limit varies apparently from c. 650 m on the windward, westerly side to c. 850 m on the leeside in the east. To quote actual figures the forest reaches to at least 730 m in the NE, to 800 m in the S (from Cave Gulch just E of Soggy Plain where the profile III was taken), and typical leeside forest up to 850 m in the E (Red Hill). Regarding the lower limit it can definitely be stated that *Phylica* forest is primarily developed on the Base but can seemingly extend quite a way down towards the strand zone in some places. There is herbarium material of *Phylica* from 1. forest furthest W (Anchorstock Bay), 2. at 100 m altitude furthest E (Sandy Point), 3. at 200 m in the S (Cave Gulch), and 4. at 250 m in the N (E of Pigbite).

One of the Tristan reports fail to mention how the *Phylica* forest shows the effects of the stormy climate. CARMICHAEL for example, even in 1818, describes how the "island tree" grows up wherever the roots can find anchorage (CHRISTOPHERSEN cites isolated *Phylica* trees at 980 m), and changes in character from being a dwarf creeping shrub or bush in the most strongly wind-exposed places to being a 6 m high gnarled tree where the habitat is more favourable. On the whole, *Phylica* forest, despite Tristan da Cunha's northerly position, is not situated very far north of the antarctic forest-limit, a condition which, according to GOOD (1947 p. 280), must probably be ascribed to wind effects, directly or indirectly. The Falkland Islands to westward and Kerguelen Island to eastward, both lying 15° more southerly are treeless, whilst Masafuera at about the same latitude has continuous forest in a zone from 300—700 m above sea level, similar to the condition on Tristan (cp. also BROCKMANN—JEROSCH 1919 p. 167).

The undergrowth consists essentially of grasses and ferns. The latter are represented by the genera *Adiantum, Asplenium, Elaphoglossum, Gymnogramma* and *Histiopteris. Nertera assurgens* and the cyperaceous species *Carex insularis* and *C. Thouarsii* and *Uncinia gracilis* also occur.

3. *The Tree-fern zone.*

There are two tree-ferns present on Tristan. The large tree-fern, *Blechnum palmiforme,* forms a continuous and nearly impenetrable scrub on the upper part of the Base to c. 800 m level. Isolated "outposts" extend to 900 m. *Blechnum palmiforme* seems otherwise to interchange with *Phylica* forest where the forest is open in character, though the *Blechnum* zone extends higher in altitude than the forest. *Blechnum* also occurs in the lowlands sparsely distributed.

The small tree-fern, *Blechnum insulare,* can extend higher up than the larger species and is found fairly generally in the *Rumex*-grasslands which form the next vegetation zone. From herbarium material it appears also to occur more generally distributed in the lower regions. The highest isolated occurrence was noted at 1000 m.

The solitary herbarium specimen of *Nertera Holmboei* was found in this zone. Among the *Cyperaceae, Carex insularis,* at least occurs fairly frequently.

4. *Rumex — Holcus grassland* c. 800—1250 m.

The diploid form of *Rumex acetosella, R. angiocarpus* (LØVE 1944 p. 9), occurs in quantity from 800 m upwards and forms a distinct belt on the steep foreslopes to the Peak. *Rumex* can form extensive areas in practically pure stand and pure *Rumex* "grassland" is noted as occurring up to an altitude of 1100 m.

Holcus lanatus occurs generally spread above the *Phylica* forest but especially commonly together with *Rumex* in this subalpine region. I will cite the analagous condition on Masafuera where the subalpine grassland is dominated by *Anthoxanthum odoratum* and *Rumex acetosella* (see later in the account for a further discussion concerning the spontaneity or otherwise of *Rumex*).

The fine meadows and grazings occurring on the Base are little utilised since the way is too steep to bring the animals from the settlement up there.

5. *Empetrum — Rhacomitrium heaths* c. 1200—1500 m.

The dominants in this low-alpine region are the endemic varieties of *Empetrum rubrum* — var. *tristanitorum,* which extends highest, and f. *pulvinatum,* which also extends downwards to moderate altitudes. *E. rubrum* s.s., in contrast, seems to be found evenly distributed from lower altitudes up to the subalpine region.

Empetrum — Rhacomitrium heaths extend in tongues down to 1150 m and similarly upwards to 1500 m. On the gravel cones (talus fans) it was noted occurring up to 1400 m and in the gulches to 1600 m together with *Lagenophora nudicaulis* and *Acaena Stangii,* both of which belong to the low-alpine region but which generally speaking do not extend higher than c. 1280 m.

Probably belonging to this belt too are: *Nertera depressa* f. *imbricata, Rostkovia tristanensis, Ranunculus Caroli, Uncinia brevicaulis* var. *brevifolia, Asplenium alvarezense, Athyrium medium, Grammitis magellanica, Hymenophyllum peltatum* var. *Menziesii, Lycopodium insulare, L. magellanicum,* and certainly many other species. Alpine heaths with a similar flora occur on Masafuera.

The high-alpine sparse cover of moss and lichen heath has little significance for these investigations and shall not be further discussed here.

Ubiquitous species.

Besides those plants which form the typical vegetation zones there is a further group of species in the Tristan da Cunha flora which do not appear to be restricted to any one zone but to have a wide distribution within several, especially the 3—4 lowermost, zones.

The most characteristic of these species is *Apium australe.* The herbarium material discloses an even distribution over the whole island from the strand up to 1050 m. Dr. CHRISTOPHERSEN has informed me that he has found it right up to 1300 m. To judge from the wet habitats this species of wild celery is a fairly hygrophilous species, a supposition which HEGI (V, 2 p. 1146) supports. The damp climate explains this plant's exceptional abundance and general distribution on Tristan da Cunha.

Further under this category are probably: *Gnaphalium Thouarsii, Hydrocotyle capitata, Cotula australis, Scirpus sulcatus* and *S. Thouarsianus.*

Among the *Gramineae, Spartina arundinacea,* "the tussock grass' is especially common. It formed man-high thickets at one time but is now almost eradicated.

Many pteridophyta also belong to this group.

Alien species.

The vegetation so far described, which includes many endemic species, is assumed to constitute the native flora of Tristan da Cunha.

So far as we know at present Tristan da Cunha was first discovered in 1506, was visited hap-hazardly until 1810 when cultivation was commenced and corn, potatoes and vegetables grown, but not till after 1816 was the island permanently and continuously settled.

Among those species which are believed to have been introduced with cultivation and first and foremost in the settlement area itself are: *Anthemis Cotula, Anagallis arvensis, Bellis perennis, Centella asiatica, Cerastium caespitosum, Chrysanthemum Leucanthemum, Gnaphalium*

luteo-album, Oxalis corniculata, Plantago lanceolata, P. major, Polycarpon tetraphylla, Prunella vulgaris, Senecio vulgaris, Solanum nigrum, Sonchus oleraceus, Stellaria media, Trifolium repens, Ulex europaeus, Veronica serpyllifolia, Verbena officinalis, Leonotus Leonurus, Juncus bufonius, J. macer, Phormium tenax, Agrostis simulans, A. tenuis, Aira caryophyllea, Anthoxanthum odoratum, Cynodon Dactylon, Lolium perenne, Poa annua, P. pratensis, P. trivialis, and *Vulpia bromoides* (cp. p. 33 for *Rumex* and *Holcus*).

Nightingale.

Here there is no differentiation into vegetation zones. *Spartina arundinacea* dominates and characterises the island's vegetation. *Spartina* springs up everywhere after burning, a fact which explains its present dominance on Nightingale as the island has been cleared by fire. *Spartina* seems on the whole to grow in much drier habitats than *Phylica,* which occupies only the most favourable localities. Thus *Phylica* follows the watercourses and forms sparse forest around Lake Region at c. 200 m altitude.

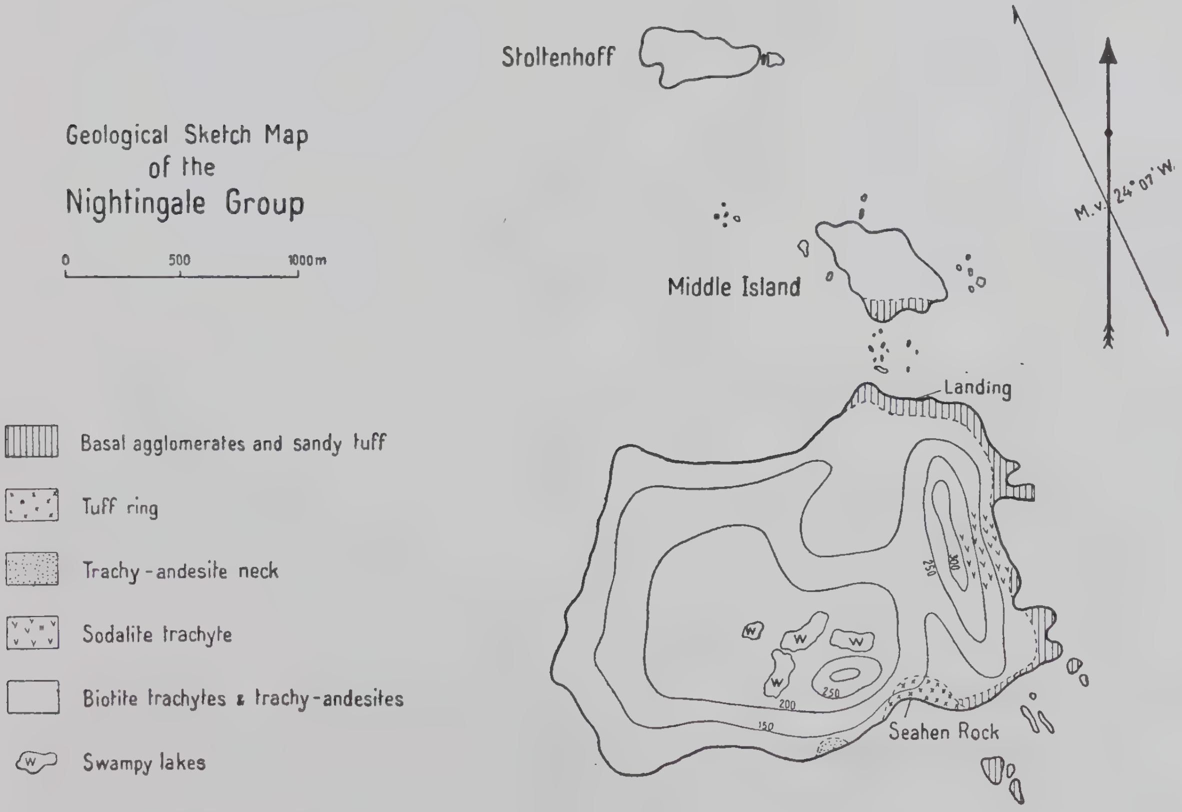

Fig. 4. Sketch map of the Nightingale group. Contour lines in metres (After Dunne 1941).

To judge from the herbarium material the number of species is substantially smaller on Nightingale than on Main Island. Both c. 25 of the native species, including the two *Empetrum rubrum* varieties, *Acaena, Lagenophora, Hydrocotyle, Uncinia, Blechnum australe* and *Lycopodium magellanicum,* and the introduced species are lacking.

Inaccessible.

This island has little importance for these investigations and consequently I shall say little more than that *Phylica* forest dominates and that the plateau bears some area of *Scirpus* grassland (moorland) together with *lichens,* shrubby *Phylica* and tree-ferns. *Spartina* occurs sparsely. The number of species is approximately the same as on Main Island.

*

I have troubled to give such an extensive account of the vegetation, even if the main object of my investigation is not phytosociological, mainly because in the pollen diagrams I have had to use whole families or groups as units.

As no comprehensive flora of the Tristan group has so far been published, the following preliminary list, which is based upon the herbarium brought back by the 1937—38 expedition, must for the time being, constitute the floristic base of my investigation. With the help of the above description of plant communities and the species list, the reader can form some idea as to which species constitute the different families and group categories and their role in the plant communities.

Species list of the herbarium material from Tristan da Cunha.

The following abbreviations are used for the various localities: Tr — Main Island, Ng — Nightingale, In — Inaccessible, MI — Middle Island, St — Stoltenhoff.

Pteridophyta.

Hymenophyllaceae:

Hymenophyllum aeruginosum (Poir.) Carm.	Tr	Ng	In
» *peltatum* » Desv. var. Menziesii (Presl.) . .	»		»
Trichomanes angustatum (Carm.)	»		»

Polypodiaceae:

Adiantum Poiretii (Wikstr.)	Tr		In		
Asplenium alvarezense (Rudm. Brown)	»		»		
» *erectum* (Bory) (f. A. *insulare* Carm.)	»	Ng	»		
» » » var. aequibasis (C. Chr.)		»			
» *monanthes* (L.)	»				
» *obtusatum* (Forst.) var. *crassum* (Thouars.) C. Chr.	»	»	»	MI	St
» *platybasis* (Kze.) var. *subnudum* C. Chr.			»		
Athyrium medium (Carm.) Moore	»		»		
Blechnum australe (L.)	»		«		
» *palmiforme* (Thouars) C. Chr.	»	»	»		
» *penna-marina* (Poir.) Kuhn.	»	»	»		
Dryopteris aquilina (Thouars) C. Chr.	»	»	»		
» *tomentosa* » O. K.	»	»	»		
Elaphoglossum hybrideum (Bory) Moore	»		»		
» *insulare* (C. Chr.)	»				
» *laurifolium* (Thouars) Moore	»	»	»		
» *obtusatum* (Carm.) C. Chr. f. *major*	»		»		
» *succisifolium* (Thouars) Moore	»	»	»		
Grammitis magellanica (Desvaux)	»	»	»		
Gymnogramma cheilanthoides (Sw.) Kaulfuss	»		»		
Histiopteris incisa (Thbg.) J. Sm. *Carmichaeliana* (Agardh.) C. Chr.	»	»	»		
Hypolepis rugulosa (Labill.) J. Sm. var. *villoso-viscida* (Thouars) C. Chr.	»	»	»		
Polystichum adiantiforme (Forst.) J. Sm.	»		»		
Vittaria Vittarioides (Thouars) C. Chr.	»	»	»		

Salviniaceae:

Azolla filiculoides (Lam.)			»		

Lycopodiaceae:

Lycopodium diaphanum (Sw.)	»		»		
» *insulare* (Carm.)	»	»	»		
» *magellanicum* (Sw.)	»				
» *selago* (L.)			»		

Angiospermae.

Liliaceae:

Phormium tenax (Forst.)	»				

Juncaceae:				
Juncus bufonius (L.)	Tr			
» *effusus* (L.)	»			
» *macer* (S. F. Gray)	»			
Rostkovia tristanensis (Christoph.)	»			
Gramineae:				
Agrostis simulans (Hemsl.)	»			
» *stolonifera* (L.)	»			
» *tenuis* (Sibth.)	»			
Aira caryophyllea (L.)	»		In	
Anthoxanthum odoratum (L.)	»			
Cynodon Dactylon (L.) Pers.	»			
Holcus lanatus (L.)	»	Ng		
Lolium perenne (L.)	»			
Poa annua (L.)	»	»	»	
» *infirma* (H.B.K.)	»			
» *pratensis* (L.)	»			
» *trivialis* (L.)	»			
Spartina arundinacea (Thomas)	»	»	»	MI
Sporobolus capensis (Willd.)	»			
Vulpia bromoides (L.)	»		»	
Cyperaceae:				
Carex insularis (Carm.)	»	»	»	
» *Thouarsii* »	»			
» » » var. *recurvata* (Christoph.)	»	»	»	
Cyperus congestus (Vahl)	»		»	
» *tenellus* (L.)	»			
Uncinia brevicaulis (Thouars)	»		»	
» » » f. *brevifolia* (Christoph.)	»			
» *gracilis* (Thouars)	»			
» » » var. *brevispicula* (Christoph.)		»	»	
Piperaceae:				
Peperomia tristanensis (Christoph.)	»		»	
Moraceae:				
Ficus carica (L.)	»			

Polygonaceae:					
Rumex frutescens (Thouars)	Tr		In		
Chenopodiaceae:					
Chenopodium Ambrosioides (L.) subsp. *euambrosioides* Aellen var. *tomentosum* (Thouars) Aellen	»	Ng	»		
Caryophyllaceae:					
Cerastium caespitosum (Gil.)	»		»		
Polycarpon tetraphyllum (Nathorst)	»				
Stellaria media (L.)	»				
Ranunculaceae:					
Ranunculus Caroli (Christoph.)	»				
Rosaceae:					
Acaena Stangii (Christoph.)	»		»		
Leguminosae:					
Trifolium repens (L.)	»				
Ulex europaeus (L.)	»				
Oxalidaceae:					
Oxalis corniculata (L.)	»		»		
Geraniaceae:					
Pelargonium acugnaticum (Thouars)	»		»		
Rhamnaceae:					
Phylica arborea (Thouars)	»	»	»		St
Malvaceae:					
Malva parviflora (L.)	»				
Umbelliferae:					
Apium australe (Thouars)	»	»	»	MI	»
Centella asiatica (L.) Urb.	»				
Hydrocotyle capitata (Thouars)	»		»		

Empetraceae:					
Empetrum rubrum (Vahl)	Tr	Ng	In		St
» » » f. *pulvinatum* (Christoph.)	»				
» » » var. *tristanitorum* (Christoph.)	»				
Primulaceae:					
Anagallis arvensis (L.)	»				
Convolvulaceae:					
Concolvulus Soldanella (L.)	»				
Verbenaceae:					
Verbena officinalis (L.)	»				
Labiatae:					
Leonotis Leonurus (L) R. Br.	»				
Prunella vulgaris (L.)	»				
Solanaceae:					
Solanum nigrum (L.)	»		»		
Physalis peruviana (L.)			»		
Scrophulariaceae:					
Veronica serpyllifolia (L.)	»				
Plantaginaceae:					
Plantago lanceolata (L.)	»				
» *major* (L.)	»				
Rubiaceae:					
Nertera Holmboei (Christoph.)			»	MI	»
» *depressa* (Banks et Sol.)	»	»	»		
» *assurgens* (Thouars)	»				

Compositae:

Anthemis Cotula (L.)	Tr				
Bellis perennis (L.)	»				
Chevreulia sarmentosa (Pers.)	»		In		
Chrysanthemum Leucanthemum (L.)	»				
Cotula australe (Less.)	»	Ng			
Gnaphalium lutes-album (L.)	»		»		
» *Thouarsii* (Thouars)	»	»	»		
Lagenophora nudicaulis (Comm.) P. Dusen	»		»		
Senecio vulgaris (L.)	»				
Sonchus oleraceus (L.)	»	»	»	MI	St

B. METHODS

1. DESCRIPTION OF SPORES AND POLLEN GRAINS.

Since very few of the spores and pollen grains which could be expected in the Tristan peats had been previously described, it was necessary therefore at the outset to prepare an extensive spore- and pollen-herbarium and to construct identification keys for those species at present growing on the islands. With Dr. CHRISTOPHERSEN'S herbarium collection from Tristan as a basis I made type slides of both pteridophytes and phanerogams, using ERDTMAN'S modified acetolysis method (FÆGRI and IVERSEN 1950).

Only those spores and pollen grains which play a part in the pollen diagrams have been described in the following section. FÆGRI and IVERSEN'S terminology (1950) has been utilised in making the descriptions.

Pteridophytes.

Lycopodiaceae.

There are two spore types in this family, foveolate, within the subgenus *Urostachya* and reticulate, within the subgenus *Rhopalostachya.* In the fossil material only *Lycopodium magellanicum* (*Rhopalostachya*) and *L. insulare* (*Urostachya*) occurred. *L. magellanicum* can be distinguished from the third species present (*L. diaphanum*) by the variability in size of mesh of the reticulum on the distal side in the former.

Hymenophyllaceae.

The family has tetrahedral spores which, in *Hymenophyllum*, are very thin-walled, and pellucid and bear very small scattered spines. *Trichomanes* on the other hand has thicker-walled spores with a pale yellow exospore which is wholly verrucate. In the fossil material there were found *Hymenophyllum peltatum* and *Trichomanes angustatum* with finely papillate spores and *Hymenophyllum aeruginosum* in which the spines are practically vestigial, c 1 μ in length and very slender.

Polypodiaceae.

Both tetrahedral and bilateral spore types are found within this family. Of the genera possessing tetrahedral spores, *Gymnogramma cheilanthoides* and *Grammitis magellanica* were discovered. The spores of *Gymnogramma* are markedly triangular, the distal side is coarsely verrucate with blunt marginal ribs. In *Grammitis* the spores are faintly triangular and coarsely gemmate.

In the fossil material it was possible to distinguish *Histiopteris incisa* and *Hypolepis rugulosa* among the bilateral spore types. *Histiopteris* has large, irregular, verrucate spores whereas those of *Hypolepsis* are densely papillate with long spines and agree entirely with SELLING'S description of *H. punctata* (SELLING 1946).

Apart from the spores described above only unidentifiable spore remains were found in which the exospore had entirely disappeared. For further discussion see p. 23.

Phanerogams.

Cyperaceae, cp. SELLING (1947) for a description of *Uncinia* and other *Cyperaceae.*

Juncaceae, cp. CRANWELL (1942) for a description of *Rostkovia* and other *Juncaceae.*

Chenopodiaceae, Chenopodium ambrosioides subsp. *euambrosioides*, is of the usual *Chenopodiaceae* type.

Rosaceae, Acaena Stangii: — This can be distinguished from *A. exigua* (which is described by SELLING 1947) by the little-pronounced equatorial thickening of the exine and by the strongly projecting pores. Furrows short and operculate. Pores strongly protruding, transversely elongated, the outer part constricted meridionally midway. Grain, spherical, oblate-suboblate. Diameter c. 28 μ. Sculpturing irregular, reticulate with very fine meshes. Exine c. 2.5 μ thick.

Rhamnaceae, Phylica arborea: Tricolporate, sub-oblate of the *Rhamnaceae* type, c. 14 × 18 μ. Very long furrows with broad margines which fuse in the polar area. Pore with annulus, slightly elongated transversely. Columellae not distinct. Sculpturing reticulate with a mesh 1.5 μ in diameter at maximum, decreasing marginally. Margines and polar area glabellate. Exine 0.5—1.0 μ thick.

Umbelliferae, Apium australe: With reference to the genus *Apium* cp. the illustrations in APER (1933). Characteristically tricolporate with transversal furrows which are constricted medially. Prolate, c. 29 × 18 μ. Exine 1.5—2.5 μ thick, somewhat thicker at the poles and less distinctly thickened equatorially.

Hydrocotyle capitata: — With reference to the genus *Hydrocotyle* cp. SELLING (1947). Tricolporate with transversal furrows. Sub-prolate, c. 28 × 22 μ. Equatorial limb circular to sub-triangular. Structure of distinct columellae between the end- and ekt-exine. Exine c. 2 μ thick, thicker at the poles. Sculpturing irregular, reticulate.

Compositae, Lagenophora nudicaulis: With reference to the genus *Lagenophora* cp. SELLING (1947). *Tubuliflorae* type. Diameter c. 35 μ. Exine thick and densely spinous.

Chevreulia sarmentosa: Tubuliflorae type. Diam. c. 25 μ. Exine with relatively densely set, short spines.

Gnaphalium Thouarsii: With reference to the genus *Gnaphalium* cp. SELLING (1947). *Tubuliflorae* type with broad furrows. Diameter c. 28 μ. Exine densely spinous.

Cotula australis: Tricolporate of *Tubuliflorae* type. Diameter c. 28 μ. Exine weakly coloured, distinctly intra-reticulate. Spines coarse and obtuse.

Pollen type X.

Tetra- to hexa-pericolpate. Subspherical. Diameter c. 35 μ. Furrows distinct, the edges irregularly dissected. No margo. Exine c. 1.5 μ thick. Columellae distinct. Sculpturing regular reticulate, diameter of the meshes less than 1 μ.

The irregular definition of the furrows gives this grain a certain resemblance to *Cyperaceae* grains, but is separated from them by having a regular spheroid shape, uniform sculpturing, coarse columellae and a somewhat thicker exine, which, to judge by the reaction to fuchsin staining, has a different chemical composition from the exine of cyperaceous pollen grains. The colour corresponds to that of ordinary pollen grains. The morphology seems to point to a dicotyledonous affinity, though agreeing with none of the pollen grains of the phanerogams growing on the islands at present.

2. FIELDWORK.

The fieldwork was carried out by Dr. CHRISTOPHERSEN in January and February 1938. He took six peat profiles of which two, *profile III, Soggy Plain, Main Island* and *profile 15, Lake Region, Nightingale Island,* were found to be in a fit state for pollen analysis.

As no peat sampler could be used, the profiles were taken directly from a peat face or excavation made for the occasion. Each profile was divided into columns of 15 to 40 cm in length. These were each supported laterally by thin strips of wood of the same length, packed carefully in newspaper or gauze, tied up at top and bottom and the top of each column clearly labelled. The material was then packed in waterproof packing cases and has so lain in store in the Botanisk museum in Oslo since 1938.

Profile III, Soggy Plain, Main Island. Collected 11-1-1938.

The profile was divided up into seven sections. The total depth of the profile was 2.49 m. Each section was cut out basally by a knife or spade, which may have produced a slight loss in continuity between each consecutive section. There was still more peat remaining below the lowest section taken.

Furthermore, the field record states that Soggy Plain lies at c. 800 m altitude, little above the tree limit. On the bog itself were a few dwarfed individuals of *Phylica,* whilst there was fairly dense *Phylica* forest some way to westward. The following species list, with estimated frequencies, was taken near to profile III.

Empetrum 10 II
Scirpus sp. 10 IV
Scirpus sp. 10 I
Lycopodium insulare 9 I
Lagenophora 10 I
Nertera 10 II—III
Apium 6 I
Holcus 9 I
Blechnum penna-marina 3 I
Carex Thouarsii 7 I
Rumex (*acetosella*) 1 I
Uncinia sp. 10 II
Uncinia sp. 2 I

Diverse *mosses, liverworts, Sphagnum* and *Cladonia.*

In addition *Spartina, Lycopodium magellanicum, Blechnum palmiforme* (both young and mature plants) are found on the bog.

Profile 15, Lake Region, Nightingale Island. Collected 7-2-1938.

Because of the danger of collapse of the excavation pit it was only found possible to take a continuous vertical profile to a depth of 2.93 m i.e. down to and including section 15. Next day the pit was emptied and re-excavated. New sections, Nos. 16—20, were taken, correlation with the first series being ensured by taking section 16 at the level of a characteristic, little humified moss layer at 2.15 m depth i.e in the middle of section 9 of the first series. Sections 16—20 were taken in vertical succession parallel with, though slightly to the side of, the vertical line of sections 1—15. Thus two sample columns were taken here, 1—15 and 16—20, which were slightly displaced laterally and had an overlap of 78 cm. It was very lucky that such an overlap was present under the moss layer level since sections 13, 14 and 15 were stated to be unreliable and thus useless for pollen analytic work. Therefore I have based the preparation of material below the moss layer on the series of sections Nos. 16—20.

The field record states no more than that the site lies at an altitude of 200 m (cp. the sketch map, where the profile was taken in the area marked with W's in Swampy Lakes). According to Dr. CHRISTOPHERSEN the bog lies in a hollow and is a typical in-filled and overgrown lake.

The vegetation is open *Phylica* forest with *tree-ferns*. The following analysis of the vegetation is based on two quadrats of 4 m^2 and does not lay claim to being complete, the intention being to give an indication of the type of vegetation.

Phylica	IV	V
Scirpus sp.	III	I
Scirpus sp.	III	IV
Nertera	III	I
Histiopteris	I	I
Blechnum palmiforme	I	I
Carex Thouarsii	I	I
Acaena	I	0
Scirpus sp.	I	I
Apium	I	I
Asplenium (*obtusatum?*)	0	I
Elaphoglossum laurifolium	0	I
Scirpus sp	0	I

Rich selection of *mosses* and *liverworts; Cladonia.*

3. LABORATORY TECHNIQUE.

During the long storage period the peat samples had become completely dried out and were stone-hard. Those peat-layers which were rich in roots, coarser plant remains and little humified mosses were, however, fairly brittle and fragile giving rise to gaps in the profiles, though in profiles III and 15 these parts too were more or less intact. On the other hand an excessive contraction in length had occurred — some sections seeming to have shrunk by at least a half of their length, often followed by a transverse fracture of the material into two or three pieces. Great care was taken both during transport from Oslo to Bergen and during the unpacking.

To render the sections easier to work, I tried to re-moisten them using water, alcohol and then glycerine, but without success — the liquids were unable to penetrate the stone-hard samples. Consequently more drastic measures were required and with the help of knife and saw analysis-samples were taken from the sections of profile 15. 89 samples were cut out, at intervals of c. 2 cm.

Profile III was so hard that it was impossible to remove individual samples, instead the whole sections of the profile were simply sawn up into slices of c. 1 cm in thickness.

All details relating to stratigraphy, such as root layers and moss layers, changes in colour and consistency etc., were noted (cp. the stratigraphic record p. 26 for profile III).

The treatment used for the majority of the samples was ERDTMAN'S modified acetolysis method. Generally the material went into solution readily after a preparatory crumbling into small fragments and subsequent cooking in a solution of KOH for a few minutes, maintained at 10 % strength. A few samples were so pure that cooking with KOH was sufficient, a treatment that as well as being much quicker also provided an opportunity to discover if contamination with recent pollen had occurred. Treatment with hydrofluoric acid was used only in one single case. The final pollen preparations were stained with fuchsin.

The total number of spores and pollen grains counted per sample varied a good deal, but I have attempted to maintain a minimum standard of counting at least 300 (cp. the pollen diagrams).

C. THE POLLEN DIAGRAMS

1. COMPOSITION.

Tristan da Cunha was virgin ground as far as pollen analytical investigations are concerned, so that it was therefore of vital importance to compose the diagrams in a sensible manner. In other words, to find out which spore and pollen types should be taken together to form the vegetational units which one assume to have covered the islands during history. On account of the isolated position of the islands there exists no useful information and material for comparison. AUER'S investigation in Tierra del Fuego and Patagonia (AUER 1933, 1941, and 1946) deal with other vegetationel units and provide no pointers as to what ought to be taken into the 100 % sum for the present work. The same difficulty applies to SELLING'S work in Hawaii (SELLING 1948) and CRANWELL and VON POST'S work in New Zealand (CRANWELL and VON POST 1936). As a consequence, being confronted with the same problem, I had to resign myself to the advice given by the latter-mentioned authors who wrote: "The ultimate law has to emerge from the pollen diagrams themselves. Thus we depended entirely on our own material".

In accordance with the working method employed, all microfossils — spores and pollen grains — were counted and noted down irrespective of whether they could be immediately identified or not. The identification, e.g. of spores, brought me up against many difficulties. The tetrahedral spores were, with their characteristic accoutrement of reticulum, marginal thickenings, presence or absence of spines etc., gratifyingly easy to identify. On the other hand it was found impossible to give either specific or generic names to the many bilateral spore types, since the identificatory characters are present on the exospore, which had generally fallen off. In case it would later prove possible to identify some of these, by use of size statistics and more detailed examination, the unidentifiable spores, lacking the exospore, were measured and arbitrarily divided into six size groups. Due to these difficulties encountered in making exact identifications only the following types were entered in the diagrams: *Lycopodium insulare, L. magellanicum* and *Grammitis magellanica,* all having tetrahedral spores, whereas the rest (with exception of some very scarse types) were lumped together under the heading "fern-spores".

Within the phanerogams I have not undertaken the difficult task of identifying the genera within the family *Gramineae.* All that I can say is that my *Gramineae* all belong within the *"wild grass"* type (FIRBAS 1937 p. 448), since the pollen grains are relatively small sized, 28—35 μ after acetolysis, which range should agree well with FIRBAS'S figures for KOH-treated grains, viz. 20—25 μ seldom 30 μ. (A specific identification, however, would have a very great importance in helping to establish the age of the immigration and spread of *Spartina,* which plays such a dominant role in the present day vegetation on Nightingale Island. Pollen production figures for *Spartina,* too, would be of value, considering the low value of the *Gramineae* curve from this diagram.)

When making the pollen counts, no generic or specific separation was made within the family *Compositae*, but later work, using recent material for comparison, showed that the presence of the genera *Lagenophora*, *Chevreulia*, *Gnaphalium* and *Cotula* could be proved in the Tristan fossil material.

As stated, when it came to constructing the diagrams there existed no earlier work on which to build, nor was the meagre knowledge of the ecology of the present constituents of the vegetation any sound basis, so there was only one solution viz. to use the method as described by CRANWELL and VON POST in New Zealand and by SELLING in Hawaii, "trial and error". The microfossils were chosen as a basis in the hope that they, or their various trial combinations, would throw some light on the history of vegetation and climate on Tristan da Cunha. A first attempt was made with exclusion of 1. *Fern spores*, 2. *Empetrum rubrum*, 3. *Cyperaceae*. However, the curves of the two first-named alternatives gave no interesting indications. On the other hand exclusion of the *Cyperaceae* from the total proved to be favourable in profile 15, where there is absolute dominance, in places over 95 %, of *Cyperaceae* pollen over a large section of the diagram. Since this dominance to a high degree mask changes in the other curves, and since it seems to be due to purely local pollen production I found it best to divide up this diagram in such a way that the *Cyperaceae* were set in relief against a background of the "other" pollen and spore type curves, viz. set in a total diagram of its own furthest to the left-hand side of the main diagram, whilst the other groups were included in a 100 % sum of their own in a partial diagram on the right-hand side. Neither this nor other selective treatments were deemed necessary in profile III.

"*European*" pollen types, *Nothofagus*, and *Plantago lanceolata* were excluded from the 100 % sum, and were indicated separately. The figures given on the right-hand side of each diagram give the total of pollen grains and spores which make up the 100 % sum for each individual sample analysed. In profile III the *Compositae* and *Phylica* were so scarce that no curve could be constructed. Their presence is indicated in the diagram by their respective initial letters and their percentages. Among other microfossils which were very sparsely represented in both profiles and are neither included in the 100 % sum nor set-out in the diagrams are the following: 1. *Acaena*, which occurred discontinuously but fairly evenly distributed in both diagrams, never exceeding 7 grains in any sample, and 2. *Chenopodium*, discontinuous with a maximum occurrence of 5 grains in a single sample.

2. DIAGRAM TYPE.

The diagrams have been executed following essentially the principles drawn up by Fægri and Iversen (1950). The diagrams are really self-explanatory and should require no further description. When individual histograms are left with blank white columns, this does not indicate that they have not been included in the 100 % sum, but that one of the group appears to be over-represented, due to the occurrence of this pollen in small clumps in the slides, so that the percentage value for the whole sample is directly misleading. In this investigation there are comparatively few constituents of the diagrams and discussion centres only around the development as a whole, the gross changes in relations, not the details. Therefore I have chosen, for the sake of clarity, to use the "dissolved" type of diagram, in this instance using histograms. Furthermore, in my opinion, the "dissolved" (dispersed) type of diagram, in which all groups are plotted individually, is less conventionalised than the "composite" type, in which all the groups are plotted from the same base-line, and is therefore better suited to investigations in new regions.

3. BOG STATIGRAPHY.

Knowledge of the bog vegetation and of peat formation on Tristan da Cunha is much too incomplete that anything definite can be said about the bog stratigraphy itself. The content of roots and the consistency of the peat presuppose terrestrial peat formation. It is consoling that Cranwell and von Post (1936 p. 314) similarly leave the question unanswered in New Zealand and for the same reasons. They write: "Because of that (deficient knowledge of the plant-associations from which the peat have resulted) we have refrained from making any systematic examination of the bog stratification, and no soils have been designated in the diagrams." Selling, too, (1948 p. 49) has withheld from detailed discussion on bog-stratigraphy in Hawaii until further investigations on peat forming vegetation types have been published.

The following extract from Dr. Christophersen's field note-book gives some impression of the stratigraphy of profile 15:

1. 24 cm with surface peat with living roots.
2. 44 cm with peat.
3. Root-remains of *tree-ferns* and *trees.*
4. 54 cm with peat.
5. Root-remains of *tree-ferns* and *trees.*

6. 93 cm with peat.
7. Moss band.
8. 115 cm peat with coarse plant-remains and cuttle-bone.
9. Compact layer.

The note-book contains no account of the stratigraphy of profile III. In my own laboratory records I had noted a description of the dried profile such as I received it for investigation in 1948, and for the sake of completeness I append it here, though these data appear to have no particular importance in connection with this work:

1. c. 0—20 cm Fresh *Sphagnum* peat and surface vegetation remains.
2. c. 20 » Transition zone.
3. c. 20—80 » Loose brown peat with root layers.
    c. 20—30 cm Coarse root layer.
    c. 30—76 » Fine rootlet layer.
4. c. 80 » Transition zone from loose brown peat to a stonehard dark peat.
5. c. 80—245 » Stonehard dark peat with more or less prominent layers of roots (probable roots of *tree-ferns*, *Empetrum* and *Phylica*).
    Rootlayer I c. 108—120 cm
    » II c. 140—152 »
    » III c. 170—198 » infrequent
    » IV c. 212—220 »
    c. 158—168 cm contains peat with a band of sand.
    c. 97—107 cm wit ha marked light brown zone with a thin darker stripe of peat at c. 102 cm.

D. INTERPRETATION OF THE DIAGRAMS

1. ZONING.

After the principles laid down by Fægri and Iversen (1950) the zone system of a pollen diagram ought to form the foundation on which all subsequent discussion of the diagram depends. L. von Post has demonstrated for the post glacial period a synchronous revertent development of both vegetation and climate practically everywhere in the world where pollen analytical investigations have been made (VON POST 1946). Together with AUER he has shown that this phenomenon of revertence has occurred in Tierra del Fuego and Patagonia. Consequently a useful aim will be to examine the Tristan da Cunha diagrams and see if the zonation established leads to any common link with these latter investigations. It is my opinion that at present we must be particularly on guard for purely local developments that may have interfered with, or masked, such large-scale and reginal phenomena that VON POST discusses. Since, too, knowledge of the bog-stratigraphy, ultimate depth of the peat and of any useful synchronous horizons is wholly lacking, the South American zonation system ought not be too rigidly or uncritically applied when creating such a system for the Tristan diagrams. I shall return to a consideration of VON POST'S system later (see p. 33). I have tried constantly to comply with the stringent demand for "completely unambiguous criteria" and have so arrived at the following zonation system as indicated in the left-hand column of the diagrams. I have chosen to deal with profile 15, *Lake Region, Nightingale Island,* first, because in this diagram the course of the curves is clear-cut and there is a well-marked division into alternating terminocratic and mediocratic elements.

Profil 15, Lake Region, Nightingale Island.

The zone boundary I—II appears completely to fulfil the above demands since all the curves undergo more or less radical changes at this level, together with the appearance of fresh elements. The terminocratic curve for *fern-spores* falls rapidly from an average value of 50 %, or more, to play a very minor role in zone II; the *Gramineae* curve steadily maintains such low values throughout the diagram that the insignificant rise at, approximately, the zone boundary cannot be used as a valid criterion for this boundary. The *Compositae* however are outstanding, being practically absent during zone I, appearing at about the zone boundary and having continuous, though admittedly low, values throughout zone II. *Pollen type X* also first occurs at about the zone boundary, thereafter attaining a dominant position during the larger part of zone II. The curve for *Apium* goes hand in hand with the *Cyperaceae* curve throughout the deposit as a whole, both curves showing in the respective diagrams a sudden rise at the boundary to values of over 60 % in zone II. The *Lycopodium* curve presents a mirror image to the *Compositae* curve, from low but continuous values in zone I to insignificant and discontinuous values in zone II. The Phylicacurve exhibits a well-marked, steep decline into zone II, in which it plays a minor role seldom exceeding the 10 % mark. The *Empetrum* curve is comparable with the *Lycopodium* curve, no *Empetrum* grains at all have been found below 163 cm. The *Hydrocotyle* curve is another similar to the *Compositae* curve, occurring for the first time just above the zone boundary.

The zone boundary II—III is not so wholly convincing, though the marked rise of the *fern-spore* curve and the decline of the curve for *pollen type X* do seem to indicate fairly deep-reaching changes. Admittedly the *Cyperaceae* curve too, in the total diagram, shows a very marked decline, but considering the very variable values shown by this curve throughout zone II and the somewhat doubtful validity of the curve as a whole render it uncertain as a boundary indicator. I cannot wholly exclude the possibility that zone III is not really just a sub-zone of zone II.

Within the individual zones themselves I have tried to set up a series of sub-zones based on the minor variations of the curves.

Sub-zone a is marked by a subsidiary increase of the *Cyperaeae* and *Apium* curves near the top of the profile. *Phylica* maintains an even curve with an average value of 30 %, while *Empetrum* is discontinuous and with low values.

Sub-zone b represents a maximum for the *Empetrum* curve and a decline to low values for *Phylica*. *Apium* is practically absent. The *Cyperaceae* curve is at minimum.

Sub-zone c marks the transition zone between zones I and II previously mentioned. The *Apium* curve's maximum falls away more or less in this sub-zone.

Sub-zone d is primarily marked by the maximum for *pollen type X* and the minimum for *fern spores*. *Hydrocotyle* forms a low, continuous curve in the middle of this sub-zone.

Sub-zone e is basically the transition region between zone II and the fully developed zone III.

Profile III, Soggy Plain, Main Island.

The course of the curves in this diagram is of such a nature that the zonation proposed is not so unambiguous as one could wish it to be, and those zones that I have put forward must be taken with reservation. The background to the zonation is in fact the attempted comparison of the two diagrams which forms the subject of the next section of the paper. It is the *Empetrum* curve, especially the maximum in sub-zone b, that first and foremost defines the zone boundary A—B. The fern spore curve declines and the *Cyperaceae* curve shows a marked rise.

The decline in the *Lycopodium* curve and a certain rise in the *Apium* curve are further indicators in favour of the proposed zonation system.

Sub-zone a is essentially characterised by the marked rise in the *Gramineae* and *Rumex* curves towards the top of the profile. The *fern spore* curve especially is depressed in consequence.

Sub-zone b marks the upper maximum in the terminocratic *Cyperaceae* curve and a simultaneous minimum of the *fern spore* curve. A steep rise in the *Grammitis* curve to values of over 10 %. The low *Empetrum* curve shows two minor advances in sub-zones a and b. The *Apium* curve rises towards the end of the sub-zone and continues so doing into the next sub-zone.

Sub-zone c primarily marks the maximum of *Apium* and the minimum of *Cyperaceae.* A good inverse relationship is shown between the various maxima and minima of the *Cyperaceae* and *fern spore* curves respectively throughout the diagram. A slight advance in the *Gramineae* curve marks the change-over to the next sub-zone.

Sub-zone d is the region of the *Empetrum* curve's maximum. The curves for *fern spores* and *Cyperaceae* have changed phase again relative to one another.

Sub-zone e is predominantly a transition region, as aforementioned.

2. SYNCHRONOLOGY.

In view of the lack of data on the ecology of the various vegetation units of the pollen diagram I feel it is necessary to state, at the outset, that the following comparison of the two diagrams rests on a more insecure base than could be desired.

During both the preparation and the analysis of the samples I was on the look-out for layers of volcanic dust, or similar stratigraphic indications, which could help us to synchronise the various profiles. A layer which appeared to consist of volcanic dust turned out, on later examination, to be no more than a sand layer.

The zonation, as well as this attempt to synchronise the two diagrams, is based on the probability that profile III represents peat formation over a shorter space of time than profile 15 represents. Although I had to give up any attempt to describe or to utilise bog stratigraphy in this connection, as discussed previously, it was the uppermost 20 cm of fresh *Sphagnum* peat in profile III which first gave me the idea that perhaps this profile represented a more rapid formation of peat than profile 15 (cp. peat stratigraphy p. 25 and 26).

I have previously tried to show (cp. sections A 2 and A 3) that the rainfall is probably greater on Main Island than on Nightingale Island, especially at the altitude of Soggy Plain. Considering the laws governing peat formation this fact would yield added support to my hypothesis

With this probability as a basis I have concluded that zone I in profile 15 is synchronous with zone A in profile III, presuming that:

The *Empetrum* max.	in profile 15 b	corresp. to the max.	in profile	III d.
The *Apium*	—»— 15 a	—»—	—»—	III c.
The *Fern spore*	—»— 15 I	—»—	—»—	III A.

The use of the *Cyperaceae* curves in similar comparisons is more dangerous on account of the effects of local pollen production causing gross over-representation, mentioned previously under profile 15. However, they too, appear to have much the same course in the two diagrams. In actual fact the distinctly terminocratic trend of the *Cyperaceae* curve within zones I and II in profile 15 can be matched in the correspondingly well-developed terminocratic curve within zones A and B in profile III. The character of the respective zone transitions is strikingly similar. Thus the same change in role between the *fern spore* curve and the *Cyperaceae* curve at the zone boundaries, in both cases, is well shown. The characteristic disappearance of the *Empetrum* curve at about this boundary level forms perhaps the most outstanding connecting point between the two diagrams. When the parallel behaviour of the *Lycopodium* curve is also taken into account, with its marked transient rise followed by an abrupt decline and later dis-continuity, some of the first scepticism about the validity of the proposed synchronisation and comparison begins to be dispelled. The rise in the *Apium* curve, and perhaps too the decline in the *Gramineae* curve, present further points of parallelity in the developments at this zone boundary in both diagrams. On the other hand the *Compositae* curve and the curve for *pollen type X* certainly do not appear to harmonise so well in the two diagrams. Since, however, the *Compositae* curve is formed of a heterogeneous group of plants (cp. section B 1) and the identity of the plant producing *pollen type X* is an unsolved riddle, this attempt to synchronise the two diagrams cannot be discounted on these grounds alone. Besides, the quantity of *pollen type* X in diagram III is insignificant as compared with that of diagram 15.

3. VEGETATIONAL HISTORY, CLIMATIC CHANGE, AND THE AGE OF THE DEPOSITS.

For similar reasons to those advanced in the preceding section it is naturally impossible to draw any wholly non-controversial conclusions about the vegetational and climatic development on Tristan or about the actual age of the peat deposits. I have, therefore, merely attempted to put forward some of my views on these subjects rather than embarking on any detailed interpretation of the diagrams.

In the preceding section I made mention of the uniform course of the *Cyperaceae* curve in the primary zone of both diagrams. In the case of profile 15 the further course of this curve in zone II can equally well be conditioned by the developmental history of the lake basin as taken to represent a fluctuation in climate and vegetation. The profile, namely, was taken from a region marked on the map as "Swampy Lakes" and, until any other interpretation can be proved, I shall continue to regard the bog as overlying an ingrown lake as previously mentioned. In consequence, the possibility that the decline in the *Cyperaceae* curve at the zone II—I transition is due to a "Verlandung", or final ingrowth of the lake, cannot be ruled out; in which case the *Cyperaceae* dominance throughout zone II could be neatly explained as representing the conditions of more or less dense reed swamp, marginal to an open lake, prevailing during this period of time. This stage in development exists in many places on Nightingale Island at the present day. Thus Dr. Christophersen has described for me the interesting vegetation, with an abundance of difficult *Scirpus* species, around the lakes of the "Lake Region" district. At present the correctness of this interpretation can be neither proved nor disproved so long as the bog stratigraphy remains unknown.

The pollination method and pollen production of the individual species contributing to the pollen sum of the pollen diagrams is of fundamental importance for any interpretation of the diagrams.

It long remained a difficulty to explain why *Phylica* was so poorly represented in profile III, despite the presence of *Phylica* forest growing just to westward of the bog and the existence of prevailing westerly winds. A closer inquiry into the pollination conditions solved the problem, because the genus *Phylica* is self-pollinated, according to Engler and Prantl (III 5 p. 397). In consequence *Phylica* pollen can scarcely be expected in the profile from Soggy Plain, which lies above the tree limit. On Nightingale Island, on the other hand, the possibility of pollen incorporation in the bog is fully present since the bog region itself, Lake Region, is covered by sparse *Phylica* forest which must simply have showered down flowers onto the bog surface, providing the necessary source for a resultant continuous *Phylica* pollen curve throughout profile 15. To state the problem in another way, on Tristan we have the regrettable, classical source of error that the sole forest tree is not represented in the pollen rain preserved in the bog: its pollen cannot become widely and evenly spread since the species is self-pollinated. The pollen diagram will, therefore, give an incorrect picture of the composition of, and changes in, the vegetation. This source of error is, luckily, compensated for to some extent by the choice of site investigated. Soggy Plain lies namely on the transition zone between two belts of vegetation, the forest belt and the tree-fern belt. Thus the possibility exists for finding registration of any upward shift in the vegetational limits. In correspondance with the conditions on Nightingale Island such a shift would have resulted in a distinct representation of *Phylica* pollen in the diagram during that period of time in which forest covered Soggy Plain and the forest limit lay at or above the altitude of the bog region. Since, however, the *Phylica* percentage in profile III never exceeds 1 % it does not appear that any such changes have, in fact, taken place during the period of time represented in this profile.

Apium seems to have played as important a part in the flora of Tristan da Cunha in former as in recent times. *Apium* occurs in many of AUER's diagrams from Tierra del Fuego and is quoted many times as being an indicator of "eine besonders reiche Flora", particularly in the period preceding, during and after eruption II in the middle of his "Melioratum"-period. A fact which seems associated with a more or less warm, moist climate (AUER 1933 p. 189—214 and p. 298). I am not in a position to answer the question of whether the *Apium* maxima described in profiles 15 and III are likewise indications of warmer and moister conditions on Tristan da Cunha.

ENGLER and PRANTL (III 8 p. 88) cite the *Umbelliferae* as having predominantly insect pollinated flowers, though in *Hydrocotyle* self-pollination is a possibility. Perhaps this implies that *Hydrocotyle* grew thickly around the open lake during the period of time represented by zone II in profile 15.

Regarding the total absence of *Empetrum* pollen below the 163 cm level in profile 15 it is difficult to exclude the possibility that this horizon represents the immigration of *Empetrum* into Nightingale Island and perhaps into the Tristan group of islands as a whole. Assuming that the proposed synchronisation of the diagrams is correct, then the above possibility is further strengthened by the behaviour of the *Empetrum* curve in profile III, viz. it becomes unimportant and wholly discontinuous at the equivalent horizon, approximately the zone boundary A—B. The profile is unforunately too shallow for us to determine conclusively whether or not the zone boundary horizon really indicates the immigration of *Empetrum* into Tristan da Cunha.

The great rise in the curves for *Gramineae* and *Rumex* towards the top of profile III, simultaneous with the appearance of *Plantago lanceolata,* can scarcely be anything other than a marked reaction to the introduction of cultivation.

As previously mentioned *Rumex angiocarpus* and *Holcus lanatus* form at the present day a separate vegetation belt, from 800 m to 1250 m altitude. Such a belt could scarcely have existed previously without being registered pollen analytically. Since *Rumex* fails to occur below c. 45 cm level in the profile and the *Gramineae* curve, too, is very modest below this level the conclusion drawn that the *Rumex-Holcus* belt became established after the settlement of the island seems justifiable.

As aforementioned, the permanent settlement of Tristan dates from the year 1816, though already in 1810 corn, potatoes and vegetables were under cultivation. This would imply that the bog has grown c. 35 cm in c. 125 years. Since the bog stratigraphy and the rate of peat formation are unknown nothing can be stated, on the basis of the above figures, as to the age of the individual diagram zones.

How, now, do these conclusions that I have reached on the vegetational history of Tristan da Cunha fall in line with VON POST's scheme of revertence mentioned in the previous section (cp. p. 27).

L. VON POST, in that paper, has taken pollen diagrams from most of those regions of the world which have been investigated pollen analytically and has been able to show that all the diagrams demonstrate the same revertent course of development with which we have been long familiar in NW Europe. As may be expected, the expression of the phenomenon has varied according to the geographical position and the type of vegetation of the particular area examined; that synchronous climatic and vegetational development has gone on in all the areas investigated seems to be beyond all doubt.

Even though little is known about the significance of the individual constituents of the vegetation the recognition is inescapable that the course of the curves in the pollen diagrams from Tristan da Cunha shows a striking similarity with their course in the diagrams that VON POST presents to demonstrate the phenomenon of revertence. The same division into three primary zones and the same contrast between terminocratic and mediocratic elements is present in the zonation and synchronisation of the Tristan da Cunha diagrams advanced in the preceding sections of this paper. Thus the post glacial "warmth period" should be represented by zone II in profile 15 and zone B in profile III and be characterised by dominance of the following vegetation units: *Apium, pollen type X, Compositae, Hydrocotyle,* and possibly *Cyperaceae.* At the present time it is somewhat hazardous to draw conclusions, from these facts, about the climatic conditions on Tristan da Cunha during the "warmth period". Those characters marked in the diagrams suggest that the circulatory conditions in any case have undergone more or less deep-reaching changes. As I shall refer to again later on (cp. p. 38), the occurrence of six pollen grains of *Nothofagus* derived by distant transport from South America imply an increased atmospheric circulation in the period following the "warmth period".

E. LONG—DISTANCE POLLEN TRANSPORT

These investigations, as will be shown presently, have added to the ever-growing number of instances of long distance transport of pollen. During the investigation of profile III, Main Island, I found six *Nothofagus* pollen grains, which were more or less evenly distributed throughout the profile viz. at the depths of 0.07 m, 0.73 m, 1.13 m, 1.56 m, 2.03 m and 2.40 m (cp. the diagram). Since *Nothofagus* is neither found as a planted tree in the Bergen region, nor had any samples of recent *Nothofagus* pollen been prepared in the laboratory, it must be quite certain that the *Nothofagus* pollen in the fossil samples could not have been due to any contamination during work.

A more careful examination of two of the *Nothofagus* pollen grains (both were present in samples which had been acetolysed using the modified Erdtman method) gave the same results for both pollen grains:

Diameter c. 38 μ, no. of pores 6, exine thickness c. 1,5 μ, exine sculpturing psileate to faintly reticulate.

For reference to more detailed descriptions of *Nothofagus* pollen the reader is referred to von Post (1929), Cranwell (1939), and Cookson (1946).

Despite the limited distribution of *Nothofagus* in the world today (cp. fig. 5) this genus has come to have a very great importance for palaeofloristic studies in the southern hemisphere. The species of

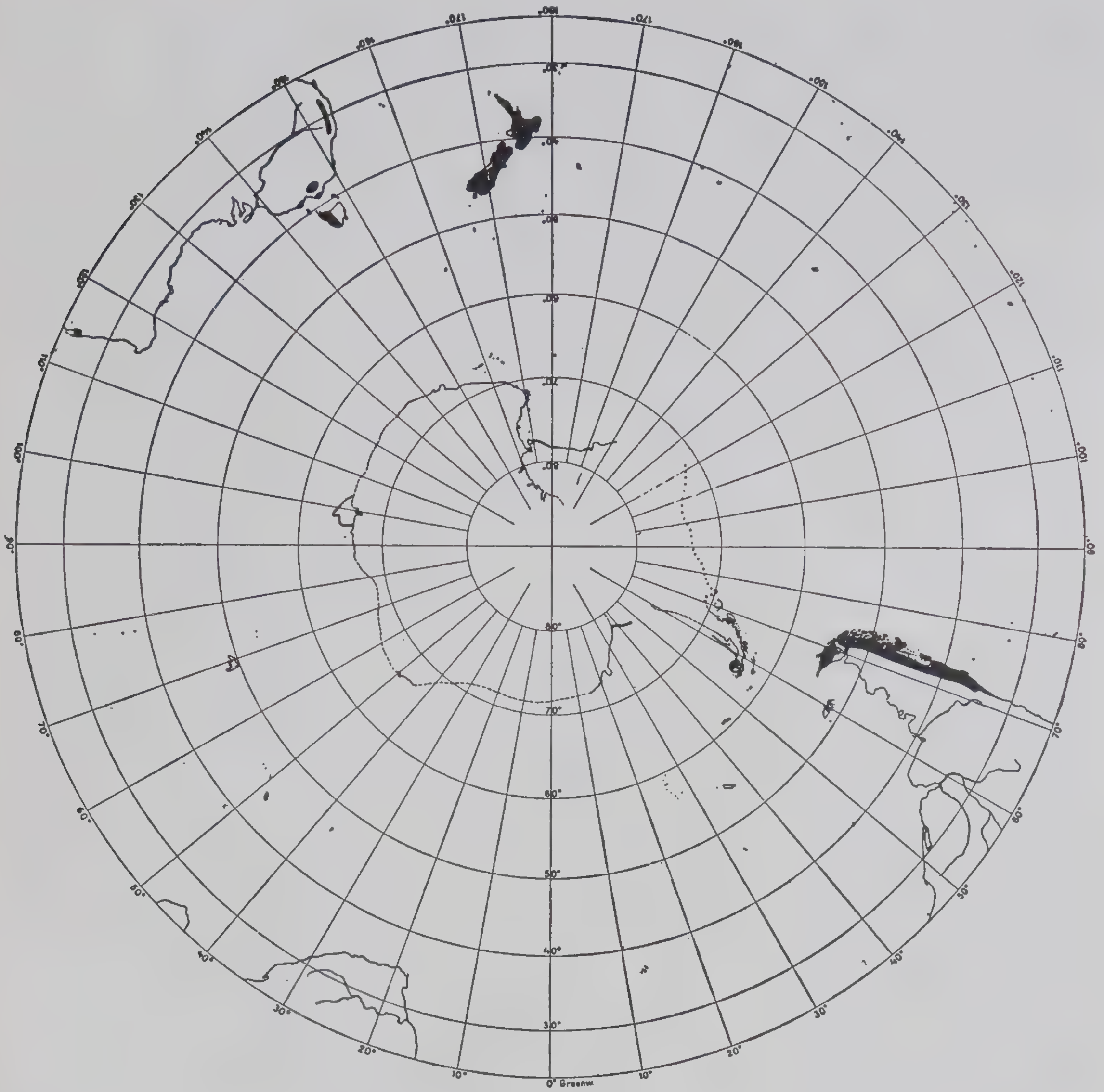

Fig. 5. Distribution of the genus *Nothofagus* Blume. The mark o on Seymour Island in Western Antarctic represents a fossil (Tertiary) occurrence (After Du Rietz 1940).

Nothofagus are, namely, dominant constituents of the temperate rain-forest in Patagonia and Tierra del Fuego and in New Zealand. The individual species, according to their respective climatic requirements, form valuable "indicator species" in studies on the history of vegetation and climate. Out of this use of pollen-analytic methods it is hoped that we can prove the former existence of many more species. In the course of such studies an identification key for the pollen types of *Nothofagus* has been prepared. From the studies of CRANWELL (1939), VON POST (1929) and COOKSON (1946) the following points emerge:

1. All *Nothofagus* pollen at present investigated, whether recent or

fossil, can on the characters of grain size, prominence or otherwise of the pores, exine thickness and other characters be divided into two groups, viz. the *Menziesii* group and the *Fusca* group.

2. Besides the above-mentioned characters the pore number is the most decisive in species determination.

3. Though the pore number admittedly varies within one and the same species one or two fixed pore numbers can be established, by the use of statistical methods, which are dominant for the particular species.

The six pollen grains I found had six pores in each instance. Unfortunately I have only mangaged to isolate and mount two of them for more critical examination and determination. Using the specific characters of VON POST (1929 p. 560) and CRANWELL (1939 p. 181 and 189) they were identified as belonging to *Nothofagus pumilio* within the *Fusca* group. Although Miss CRANWELL'S description is based on pollen of *N. pumilio* which has been treated with KOH the size of the fossil grains agrees well enough with the former, allowing for the swelling of the grains to be expected on acetolysis treatment: She gives the diameter as c. 36 μ and the exine thickness as c. 1.2 μ. An identification made from COOKSON'S key for fossil *Nothofagus* from Australia work out as "*Nothofagus sp. C*" (COOKSON 1946 p. 55).

Nothofagus does not grow on Tristan at the present day and the few scattered pollen grains which I have found in profile III demonstrate that the genus has not been present on the island within the space of time represented by the 2.45 m of peat of the profile either. I shall now set out some of the facts which seem convincing proof that we are here dealing with transport of pollen over a unexpectedly long distance.

Nothofagus to-day is a small genus represented by 16 species and restricted to the south temperate zone. Fig. 5 indicates the very limited present-day world distribution of the genus. According to CRANWELL (1939 p. 181) it appears that the *Fusca* group is dominant in South America. L. VON POST (1929) and later AUER (1941) have plainly proved the distribution of the *Nothofagus* species, among which is *N. pumilio* which interests us in the present case, in Patagonia and Tierra del Fuego throughout the quarternary period. *Nothofagus* is apparently a forest tree in the south-westerly region and *N. pumilio* is that species which extends furthest eastwards in that it forms the transition, as "wald-inseln" or scattered copses, from the forest region to the Patagonian steppe. Regarding the distribution of the individual species of *Nothofagus* in Patagonia and Tierra del Fuego cp. SKOTTSBERG 1905 Taf. 5.

Nothofagus is certainly wind-pollinated, but as far as I can ascertain there exist no published data on its actual pollen production. Perhaps the photograph taken by SKOTTSBERG (CRANWELL 1939 plate 42) in New Zealand implies that the pollen production is very high. It was not without reason that SKOTTSBERG and his companions at first mistook for a cloud of smoke enormous quantities of pollen that were observed, one late afternoon, rising skyward over the mixed beech forest. In reality such clouds of *Nothofagus* pollen need only indicate a solitary, rapid and unified pollen dispersal and are not, strictly speaking, any evidence that *Nothofagus* has a larger pollen production than other trees whose pollen dispersal, i. e. flowering period, extends over a longer period. Furthermore there seems to be a definite period intervening between years of maximal flowering in *Nothofagus,* as in *Fagus.*

The literature on *Nothofagus* is unfortunately so sparse that I have not been able to find any data on the flowering period, except the fact that *N. pumilio* and the other east South American *Nothofagus* species are deciduous. Here, as is well-known, is a region of deciduous summer forest and it would appear admissible to assume that the flowering period occurs in the spring or early summer (i. e. October—November). This implies that the flowering period will fall at a time of year when convectional air-currents are the prevailing condition normally, though such air-currents can well arise at any period of the year and therefore a spring flowering period is no necessary condition for the occurrence of long distance transport of the pollen.

The following conditions are of special importance regarding wind pollination and transport of *Nothofagus* pollen:

1. The male flowers are produced in such numbers that *Nothofagus* forest appears golden during the flowering period (the anthers are golden brown in colour).
2. The deciduous species of *Nothofagus* flower before the foliage appears.
3. Flowering, as aforementioned, appears to be very sudden and unified.
4. The discoid form of the pollen grains provides them with an unusually good ability to float in the air.

Finally I will draw attention to the fact that both the South American *Nothofagus* region and Tristan da Cunha lie within the sphere of influence of the westerly winds, such that the conditions for the transport of pollen should be optimal.

Considering the facts of wind pollination, the sudden onset of pollination, the suitability of the pollen grains for wind transport in *Nothofagus* and the effective wind system, possibly aided by the strong convection currents during the spring or early summer flowering period, the conclusion must surely be that the six *Nothofagus* pollen grains found in the peat profile from Tristan da Cunha must have been transported here from the South American *Nothofagus* forests. *This implies a transport of pollen over a minimum horizontal distance of 4500 kilometres,* a long-distance transport of pollen without parallel in the literature at present. Taking into consideration the exceptionally minute area which each analysis sample represents, of the order of a few square millimetres, one gains some real idea of the quantitative dimensions of this long-distance transport.

As mentioned previously it has been found impossible to say anything about bog stratigraphy in these profiles and it is thus equally impossible to set these pollen grains in any closer relation to the history of development of the bog. Nor, so far as I can see, have these samples in which *Nothofagus* pollen occurred any special connection with any particular features in the pollen diagram.

One feature is, however, so striking as to provoke further discussion. Five out of the six distant transported *Nothofagus* pollen grains were found within zone A whilst the sixth was found in zone B though near to the transition A—B. All were found within profile III. Following on the discussion in section D this fact implies that this long distance transport has occurred essentially within the period following the post glacial "warmth period". Unfortunately *Nothofagus* pollen has not yet been found in profile 15. If one, despite the scant basis of the evidence, dare follow this line of argument further, the conclusion is as already anticipated in the final part of section D; namely that the atmospheric circulation and thus the activity of the westerly wind belts was strengthened at the close of the post glacial "warmth period". Such a strengthening of the effect of the westerly wind belt in the latitude of Tristan da Cunha can be considered as deriving from a direct strengthening of the wind system as much as from a strengthening of the westerly wind belt, all being considered in relation to the circulatory conditions as they existed during the "warmth period" itself.

The "*European pollen*" of profile III (cp. diagram) includes *Alnus, Betula* and *Pinus* and is presumably to be ascribed to contamination during the laboratory work.

SUMMARY.

Tristan da Cunha is a storm-swept small group of islands lying wholly isolated in mid-Atlantic at latitude 37° S. and having a warm temperate climate with very heavy rainfall. There are three islands in the group, of which Main Island, rising to 2006 m altitude, is of particular interest for these investigations. The flora can be divided into six vegetation zones: a strand zone, a forest zone possessing one dominant only viz. *Phylica arborea, tree-fern* scrub, sub-alpine *Rumex-Holcus* grassland, low-alpine *Empetrum-Rhacomitrium* heath, and a high-alpine sparse cover of *moss* and *lichen.* The vegetation on Nightingale Island is dominated by *Spartina arundinacea,* with a wilderness of bog and thin *Phylica* forest in the wetter places.

Two profiles were investigated pollen-analytically, *profile* III, *Soggy Plain, Main Island,* and *profile 15, Lake Region, Nightingale Island.* Before the actual pollen analyses were made, a herbarium of relevant spores and pollen grains was made, using Dr. CHRISTOPHERSEN'S herbarium from Tristan da Cunha as a basis. An identification key was drawn up and detailed descriptions made of all spores and pollen grains not hitherto recorded in the literature.

In the pollen diagram to profile 15 the *Cyperaceae* were plotted separately since they appear to be strongly over-represented.

An attempt to give details of bog-stratigraphy was discontinued because the peat samples had become too dry during storage.

Profile 15 was divided into three zones, I, II, III, with five subzones, a, b, c, d, e, on the basis of the terminocratic character of the *fern-spore* curve, the upper terminocratic part of the curves for *Empetrum* and *Lycopodium,* and the mediocratic character of the curves for *Apium, Compositae, Cyperaceae* and *pollen type X.* On similar grounds the diagram for profile III was divided into two zones, A, B with five subzones a, b, c, d, e.

Because of the great similarity in the development and relation of all the curves in the primary zones of both diagrams zone I in profile 15 has been considered equivalent synchronous, with zone A of profile III.

I have been unable to make a detailed interpretation of the diagrams as no investigations of the ecology of the vegetation have been carried

out. However, I have indicated certain points of view: Profile 15 probably represents open lake conditions with marginal cyperaceous reedswamp in zone II, followed by the natural infilling and overgrowth of the lake at the transition to zone I. Although there is dense *Phylica* forest just to westward of Soggy Plain, *Phylica* pollen is practically unrepresented in profile III. This is not altogether unexpected since *Phylica* has cleistogamic flowers. The satisfactory *Phylica* curve in profile 15 is due to the presence of sparse *Phylica* forest growing on the bog area itself.

It is suggested that *Empetrum* immigrated into Tristan da Cunha at the transition period of zones II—I respectively zones B—A in profile III, since the pollen first occurs in the profiles at about these levels.

The maxima for the *Gramineae* and *Rumex* curves, together with the appearance of *Plantago lanceolata* pollen, suggest that zone A—a in profile III is influenced by the introduction of cultivation. Whether the *Rumex angiocarpus-Holcus* vegetation zone contributed to these curves, thus implying that this vegetation type became established as a consequence of cultivation, or whether the vegetation zone was already established before colonisation of the island began, cannot at present be settled with certainty.

The diagrams from Tristan da Cunha, following the zoning and synchronising I have adopted, show a striking similarity with the scheme of revertence that von POST has demonstrated, practically speaking, the world over wherever pollen analytic investigations have been made (VON POST 1946). The diagrams show the same prime division into three major zones afforded by the contrast between terminocratic and mediocratic elements. Therefore I consider it most probable that the post glacial "warmth period" is represented in Tristan da Cunha by zones II and B in profiles 15 and III respectively.

Six pollen grains of *Nothofagus* were found, evenly distributed, in profile III, and which, according to VON POST (1929) and CRANWELL (1939), appear to belong to *N. pumilio.* On the grounds of *Nothofagus*'s excellent adaptation to wind-pollination and the favourable prevailing wind system these grains assumedly have been derived from the *N. pumilio* forests in Tierra del Fuego and Patagonia. This presents a long distance transport of pollen over a horizontal distance of at least 4500 kilometres.

The "revertence" phenomenon shown in the diagrams and the presence of these distant transported *Nothofagus* pollen grains only in the post-"warmth period" section of the diagram are both evidences which suggests that the circulatory conditions were otherwise, and the influence of the westerly wind belt over Tristan da Cunha were somewhat weaker, during the post glacial "warmth period".

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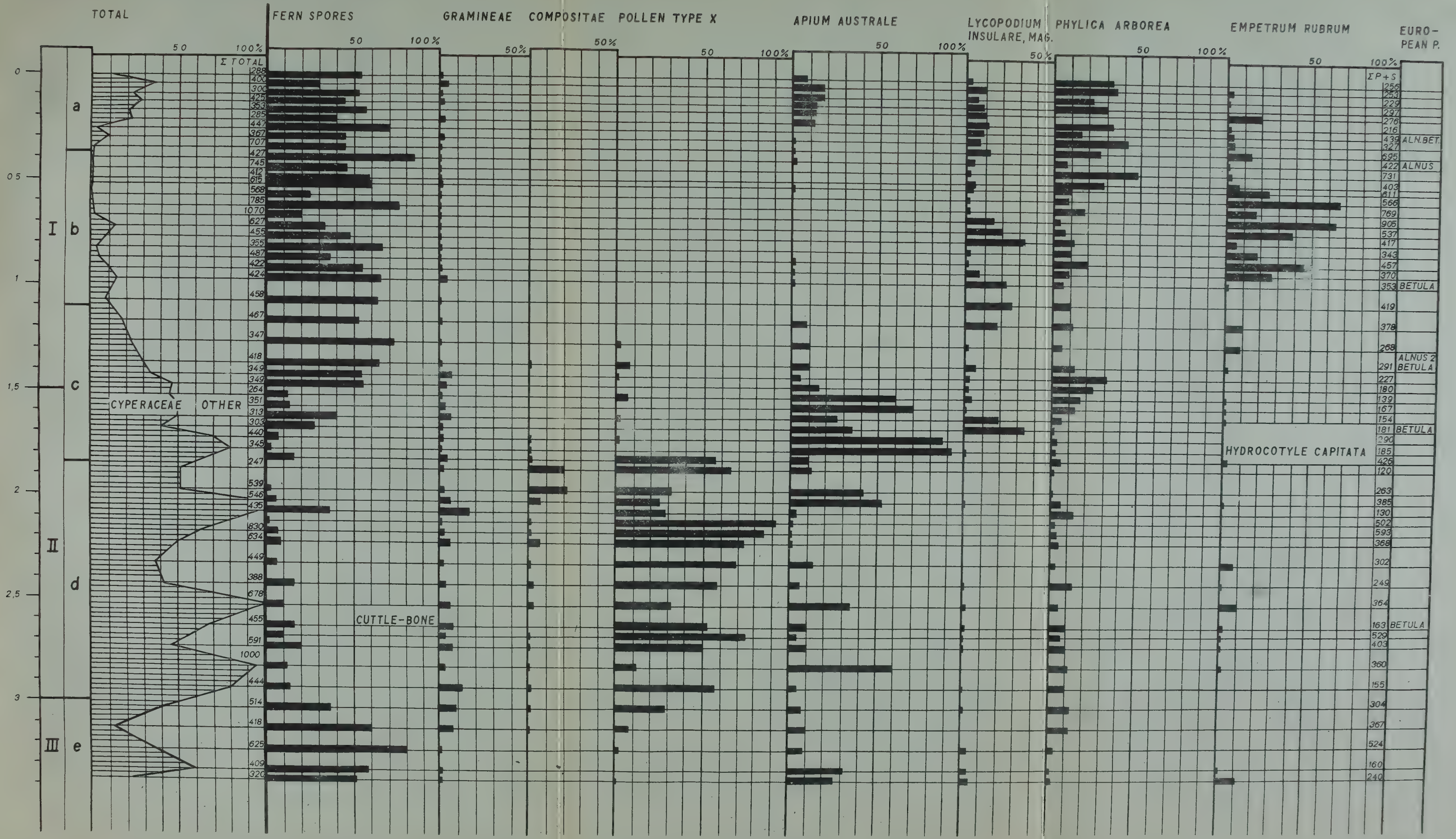
PROFILE 15, LAKE REGION, NIGHTINGALE ISLAND



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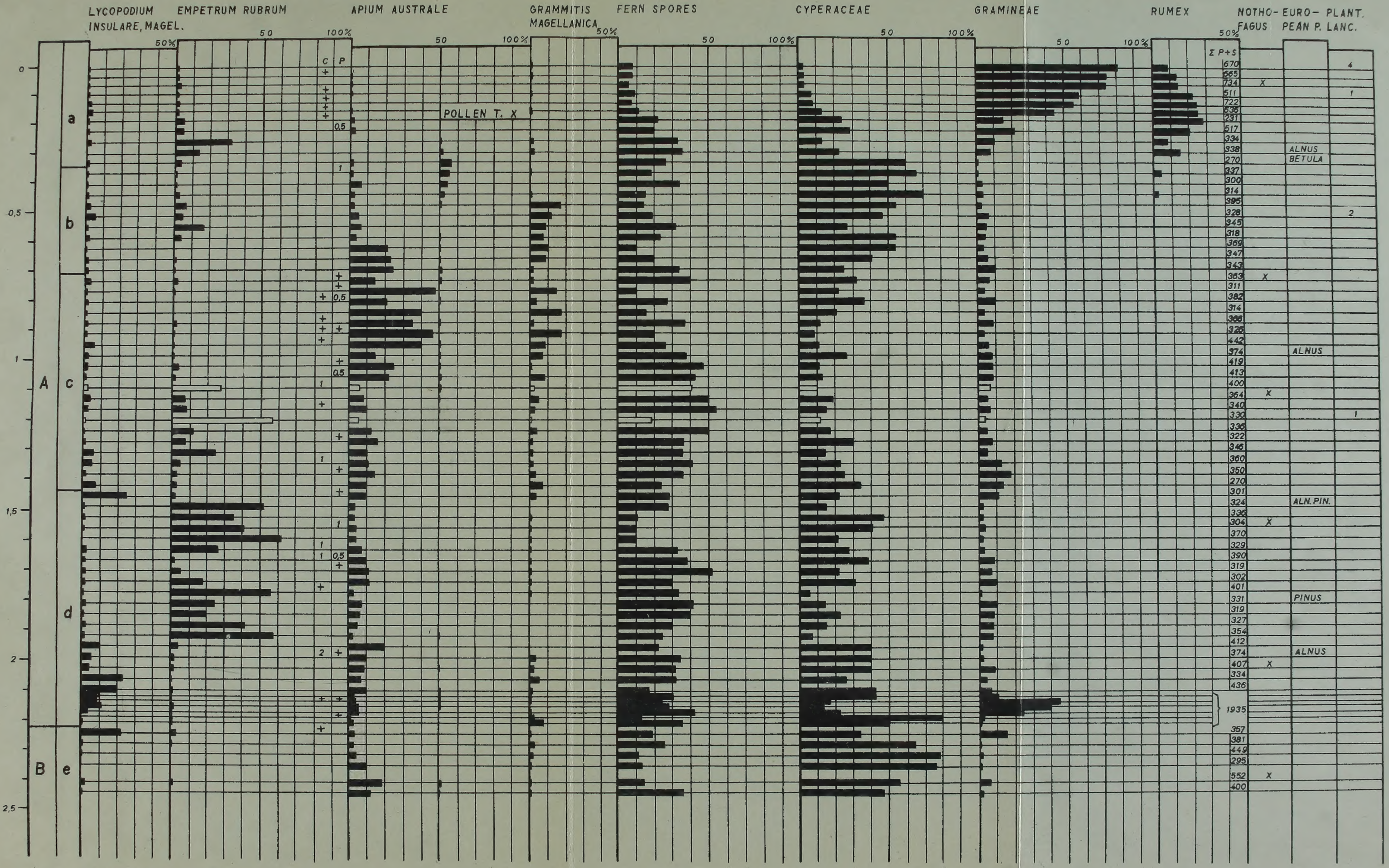
PROFILE III, SOGGY PLAIN, MAIN ISLAND



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